

**LIFE HISTORY AND DESCRIPTION OF ADULTS AND IMMATURE STAGES  
OF *GOEDENIA STENOPARIA* (STEYSKAL) (DIPTERA: TEPHTRITIDAE) ON  
*GUTIERREZIA CALIFORNICA* (DE CANDOLLE) TORREY AND A. GRAY  
AND *SOLIDAGO CALIFORNICA* NUTTALL (ASTERACEAE)  
IN SOUTHERN CALIFORNIA**

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*Abstract.*—*Goedenia stenoparia* (Steyskal) is an oligophagous, multivoltine fruit fly (Diptera: Tephritidae) that feeds in the flower heads of hosts belonging to the family Asteraceae, tribe Astereae, and subtribe Solidagininae, like all other known hosts of *Goedenia* spp. Newly reported hosts are *Ericameria parishii* (E. Greene) H. M. Hall, *Gutierrezia californica* (de Candolle) Torrey and A. Gray, *Hazardia squarrosa* (Hooker and Arnott) E. Greene, *Lessingia glandulifera* A. Gray, and *Solidago californica* Nuttall. Variations in taxonomic characters of adults are described. The third-instar larvae and puparia are described and figured, and selected characteristics of these stages are compared with the same stages of three other species of *Goedenia*. The prothorax and gnathocephalon of the third instar is smooth and mostly free of the minute acanthae that circumscribe most other body segments. The third instar of *G. stenoparia* lacks oral ridges, as do the third instars of three other congeners studied to date. The anterior thoracic spiracle bears two papillae. Minute acanthae cover the center of the truncated, posteriorly sclerotized, caudal segment, that also is perforated by scattered pores, and this central area is ringed by concentric, incomplete series of shallow, elliptical depressions. The life cycle is of the aggregative type. Overwintering limitedly occurs as sexually immature adults, but mainly in dead flower heads as prepupal third instars and puparia in apically open, vasiform cells consisting of floret and achene fragments glued together with dried liquid feces and sap. Overwintered puparia of *G. stenoparia* were parasitized by chalcidoid Hymenoptera in the genera *Eurytoma* (Eurytomidae), *Pteromalus* (Pteromalidae), and *Torymus* (Torymidae) as probable, primary, solitary, larval-pupal endoparasitoids.

*Key Words:* Insecta, *Ericameria*, *Goedenia*, *Gutierrezia*, *Hazardia*, *Lessingia*, *Solidago*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of adults and immature stages, flower-head feeding, aggregative life cycle, seed predation, parasitoids

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Most indigenous, western North American Myopitini (Diptera: Tephritidae: Tephritinae) formerly assigned to the Palearctic genus *Urophora* Robineau-Desvoidy were redesignated as *Goedenia* by Freidberg and Norrbom (1999). To date, the life

history and immature stages of three of the eight known species of *Goedenia* have been described in detail, i.e., *G. timberlakei* (Blanc and Foote), *G. rufipes* (Curran) and *G. setosa* (Foote) by Goeden et al. (1995) and Goeden (2002a, b), respectively. This

paper describes the life history and selected immature stages of a fourth species, *G. stenoparia* (Steyskal).

#### MATERIALS AND METHODS

The present study utilized specimens of adults reared from 1-liter samples of mature flower heads of *Gutierrezia californica* (de Candolle) Torrey and A. Gray collected south of Banner along Chariot Canyon Road at 940 m elevation and *Solidago californica* Nuttall at Banner at 820 m elevation in northeastern San Diego County, California. The life history study and description of the immature stages of *Goedenia stenoparia* were based in large part on dissections of samples of live mature and dead overwintered flower heads of both hosts collected during 1994–1997. One-liter samples of flower heads containing the larvae and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Twenty-six, third-instar larvae and four puparia dissected from flower heads of *S. californica* were preserved in 70% EtOH for scanning electron microscopy (SEM). Prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, studied and digitally photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Adults reared from isolated prepuparia and puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and

provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity in the insectary of the Department of Entomology, University of California, Riverside, at  $25 \pm 1^\circ\text{C}$  and 14/10 (L/D) photoperiod. Five pairs of virgin males and females obtained from *G. californica* and 10 pairs obtained from *S. californica* in emergence cages were held in each of 15, clear-plastic, petri dishes each provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2001a, b, c; 2002a, b), Goeden et al. (1993), Goeden and Headrick (1992), Goeden and Norrbom (2001), Goeden and Teerink (1997), Headrick et al. (1996), Teerink and Goeden (1999), and our earlier works cited therein. Means  $\pm$  SE are used throughout this paper. Digitized photographs used to construct text figures were processed with Adobe Photoshop® Version 6.

#### RESULTS AND DISCUSSION

##### TAXONOMY

Adult.—*Goedenia stenoparia* was described in the genus *Urophora* by Steyskal (1979) from a single male collected by E. I. Schlinger from Glendale in Los Angeles, California, on 30.vii.1955. Freidberg and Norrbom (1999) reclassified it along with most other indigenous, western North American species formerly placed in *Urophora* as *Goedenia*. Steyskal (1979) provided a drawing of the wing and Foote et al. (1993) figured the wing pattern and the head and thorax in lateral view.

A total of 211 specimens of adults reared from five hosts, i.e., 72 from *Gutierrezia californica* (de Candolle) Torrey and A.

Gray, four from *G. microcephala* (de Candolle) A. Gray, 16 from *G. sarothrae* (Pursh) Britton and Rusby, 93 from *Hazardia squarrosa* (Hooker and Arnott) E. Greene, and 26 from *Solidago californica*, were examined to estimate variation in the main characters used to distinguish *Goesdenia stenoparia*. Foote et al. (1993) stated that "From all native *Urophora* [i.e., *Goesdenia*] species with a distinctively banded wing pattern and primarily yellow scutellum, *stenoparia* is distinguished by the narrow wing bands, the failure of the discal band to attain the hind margin of the wing . . . , and the nearly complete break in the subapical band along vein M . . . ."

One third of the 211 specimens examined had a black scutellum; the central third or half of the scutellum of the remaining flies were yellow or tawny yellow. The discal band attained the hind margin in 78 (37%) of the 211 flies, but the part posterior to vein  $Cu_1$  is faint posteriorly in all but 15 (5%) of the 211 flies, i.e., seven males and eight females. It is noteworthy that the discal band was broken in cell dm in 71 (34%) flies, i.e., 57 males and 14 females, and was narrow and/or faint in cell dm in an additional 38 (18%) flies, including 20 males and 18 females. In addition, the discal band in 13 of the 71 flies, i.e., nine males and four females, also was broken in cell  $r_{2+3}$  or was faint and/or narrow in  $r_{2+3}$  in seven more flies. Finally, one male and two females (0.1%) had the discal band intact in cell dm, but broken in cell  $r_{2+3}$ .

The presence of a nearly complete break in the subapical band along vein M as a diagnostic character also showed variation. Only 74 (36%) of 207 adults, i.e., 43 males and 31 females, examined for this character showed a complete or "nearly complete" break.

Another distinguishing character ascribed to *G. stenoparia* by Steyskal (1979) and Foote et al. (1993) is the notopleuron yellow or tawny at the base of the posterior notopleural seta. This character was emphasized in Figure 507 in Foote et al. (1993).

In 64 (30%) of the 211 flies, i.e., 31 males and 33 females, the area at the base of this seta was dark brown or black.

Foote et al. (1993) described the legs as yellowish, with only the hind femur slightly darkened basally. The legs of all but one of 210 flies examined for this character would better be described as tawny; moreover, 45 (21%) of these flies, i.e., 34 males and 11 females, had a more extensively darkened hind femur, including some with a substantial basal darkening of all femora, and two males with a dark basal part of the tibia.

Finally, only 31 (15%) of the 209 flies examined had the gena not more than 1/5 as high as the eye as suggested by Foote et al. (1993), the remaining flies showing ratios of 0.20–0.27 times the height of eye. Thus, this character definitely is too variable to use to distinguish *G. stenoparia*.

Although adults of *G. stenoparia* show considerable variation, they usually can be separated from *G. caurina* by a combination of the reduced and fragmented wing pattern and the extensively darkened legs. Likewise, specimens of *G. formosa* are readily distinguished by their wider and complete discal and subapical bands that extend to the hind wing margin. A hyaline spot often present in the apical band in cell  $r_{4+5}$  also distinguishes many specimens of *G. formosa* (my unpublished data). Furthermore, the host plants of *G. caurina* and *G. formosa* in southern California differ from those of *G. stenoparia*, as reported below.

Immature stages.—*Egg*: Twenty-nine eggs dissected from immature inflorescences of *Solidago californica* (Figs. 4A, B) were white, smooth, elongate-ellipsoidal,  $0.56 \pm 0.03$  (range, 0.52–0.58) mm in length and  $0.16 \pm 0.01$  (range: 0.14–0.16) mm in width, with a 0.02-mm, peglike pedicel at tapered, anterior end. Anterior end smoothly rounded.

The eggs of *G. stenoparia* on average were slightly longer and wider than the ova of *G. timberlakei* (Goeden et al. 1993) and only slightly longer and narrower than

those of *G. rufipes* (Goeden 2002a), but otherwise generally agreed with published descriptions of those species.

*Third instar larva:* Elongate-ellipsoidal, roundly tapered anteriorly, bluntly truncated posteriorly (Fig. 1A), integument white, but venters of meso-, metathorax, and abdominal segments A1–A4 with dark brown to black infuscation (Fig. 4C); caudal segment dark brown or black; minute acanthae, apically pointed or rounded, conical and posteriorly directed (Figs. 1B-1 D-2; 2A-2) or hemispheroidal (Figs. 1B-2, 2D-1, 3B-1, C-2, D-2), circumscribe anterior fifth of meso- and metathorax, all but pleura and posterior fifth of abdominal segment A-1, posterior four-fifths of abdominal segments A2–A7, excluding pleura of A7, and cover all eight venters thereof, and posterior, truncated surface of caudal segment (Fig. 4A-1); prothorax smooth, but venter with flattened, posteriorly directed minute acanthae (Fig. 1D-1), and circumscribed by inner, medial ring of verruciform sensilla (Fig. 1C-1) and outer, incomplete ring of unpaired, verruciform sensilla (Fig. 1C-2); gnathocephalon (Figs. 1C-3, 1D) conical and medially divided by vertical cleft (Fig. 1D-2), dorsal sensory organ well-defined, hemispherical (Figs. 1D-3, E-1); pores above and dorsolateral of each dorsal sensory organ (Fig. 1D-4), anterior sensory lobe (Figs. 1D-5, E-2) bears terminal sensory organ (Figs. 1D-6, E-3); lateral sensory organ (Fig. 1E-4), supralateral sensory organ (Fig. 1E-5), and pit sensory organ (Fig. 1E-6); two medial, integumental petals (Fig. E-7); four, papilliform, lateral integumental petals (Figs. 1E-8, F-1) above each mouthhook (Figs. 1D-7, F-2), stomal sense organ (Figs. 1D-8, F-3) ventrolateral of anterior sensory lobe; mouthhook bidentate (Figs. 1D-7, F-2), anterior tooth concave posteriorly (Fig. 1F-4); median oral lobe laterally compressed, apically pointed (Figs. 1D-10, F-5), separated from labial lobe (Fig. 1F-6); anterior thoracic spiracle on posterior margin of prothorax bears two doliform papillae (Figs. 1C-4, 2A-1, B-1);

mesothoracic, lateral spiracular complex with six verruciform sensilla in vertical series (Fig. 2B-2), mesothoracic spiracle not seen; metathoracic lateral spiracular complex with nearly closed, lateral spiracle (Figs. 2B-3, C-1) and four verruciform sensilla in vertical series (Fig. 2B-4); lateral spiracular complex of first abdominal segment with partially closed spiracle (Figs. 2B-5, D-1) and five verruciform sensilla in vertical series (Fig. 2B-6); caudal segment with pair of posterior spiracular plates (Figs. 3A-1, B) surrounded by hemispherical minute acanthae (Figs. 3A-2, B-1, C-2, D-2) interspersed dorsally and medially with open pores (Fig. 3A-3, B-4), these structures ringed by two incomplete, concentric series of shallow, elliptical depressions (Fig. 3A-4), with two tapered stalex sensilla (Figs. 3A-5, C-1) and a verruciform sensillum (Figs. 3A-6, D-1); dorsolateral to each posterior spiracular plate; posterior spiracular plate (Figs. 3A-1, B) bears three smoothly flattened rimae (Fig. 3B-2), ca. 0.01 mm in length, and four spinose, interspiracular processes, each ca. 0.005 mm long (Fig. 3B-3).

The habitus of the third instar of *G. stenoparia* (Fig. 1A) resembles those of *G. timberlakei* (Goeden et al. 1995), *G. rufipes* (Goeden 2002a) and *G. setosa* (Goeden 2002b). In all four species, the venters of the thorax, anterior abdominal segments, and the caudal segment are darkly pigmented (Figs. 5D, E; Goeden et al. 1995; Goeden 2002a, b) and minute acanthae circumscribe the meso- and metathorax and abdomen, and especially noteworthy, the central, posterior surface of the caudal segment, which also is dotted with scattered pores (Figs. 3A-2, B-4; Goeden et al. 1995; Goeden 2002b). This central area is ringed by concentric series of shallow, elliptical depressions in all four species (Figs. 3A-2, B-4; Goeden et al. 1995; Goeden 2002b). The prothorax and gnathocephalon of *G. timberlakei* and *G. rufipes* are smooth and free of minute acanthae; whereas, the prothoracic venters of *G. setosa* (Goeden

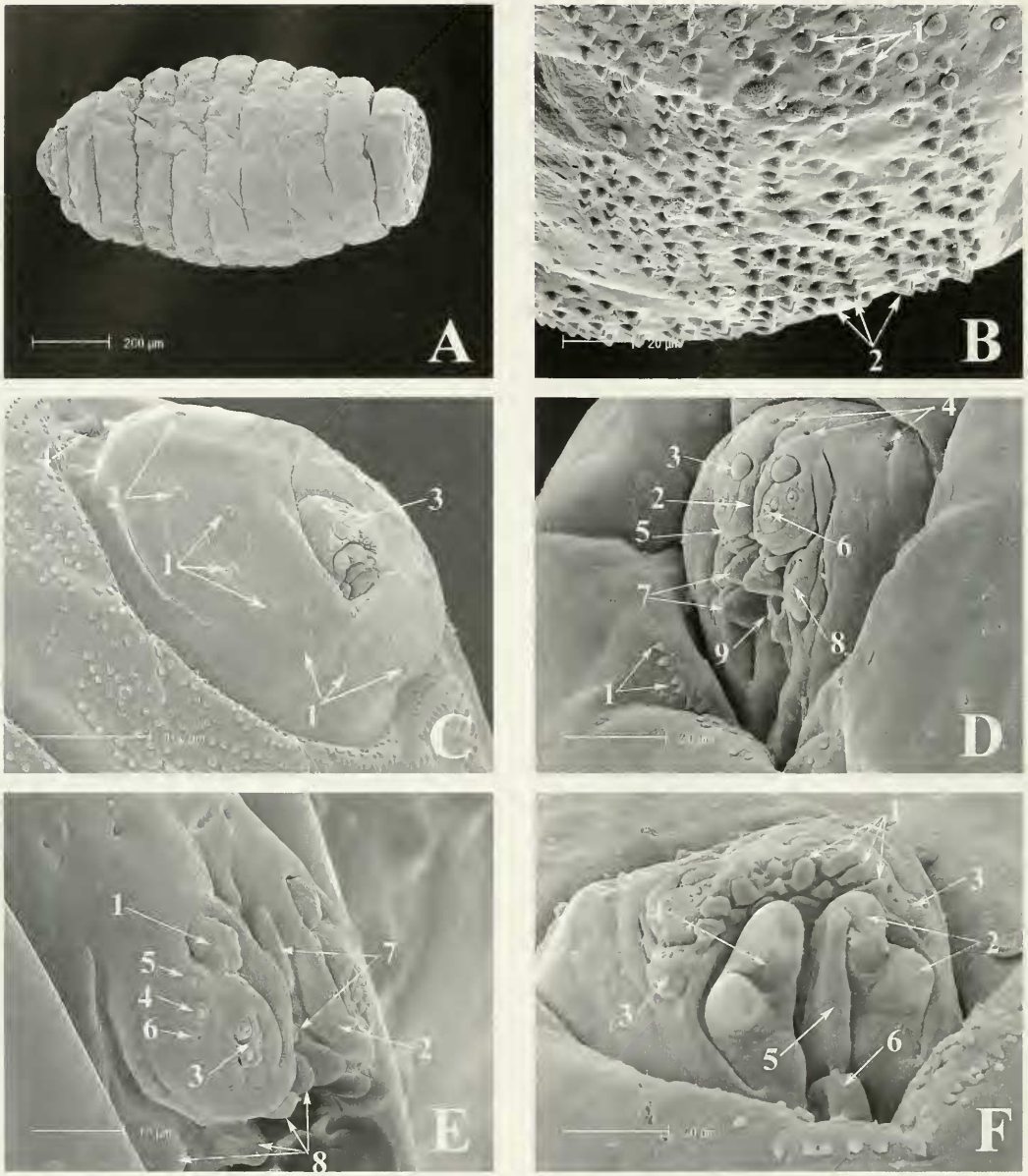


Fig. 1. Third instar of *Goedenia stenoparia*: (A) habitus, anterior to left; (B) minute acanthae on venter of abdominal segment A6, anterior to left; (C) gnathocephalon and prothorax, frontal view, 1—verruciform sensilla of inner ring, 2—verruciform sensilla of incomplete, outer ring, 3—gnathocephalon, 4—anterior spiracle; (D) gnathocephalon, frontolateral view, 1—minute acanthae, 2—vertical, medial cleft, 3—dorsal sensory organ, 4—pores, 5—anterior sensory lobe, 6—terminal sensory organ, 7—mouthhooks, 8—stomal sense organ, 9—median oral lobe; (E) 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—medial integumental petals, 8—lateral integumental petals; (F) oral cavity, ventral view, anterior at top, 1—lateral integumental petals, 2—mouthhook, 3—stomal sense organ, 4—posterior concavity on anterior tooth of mouthhook, 5—median oral lobe, 6—labial lobe.

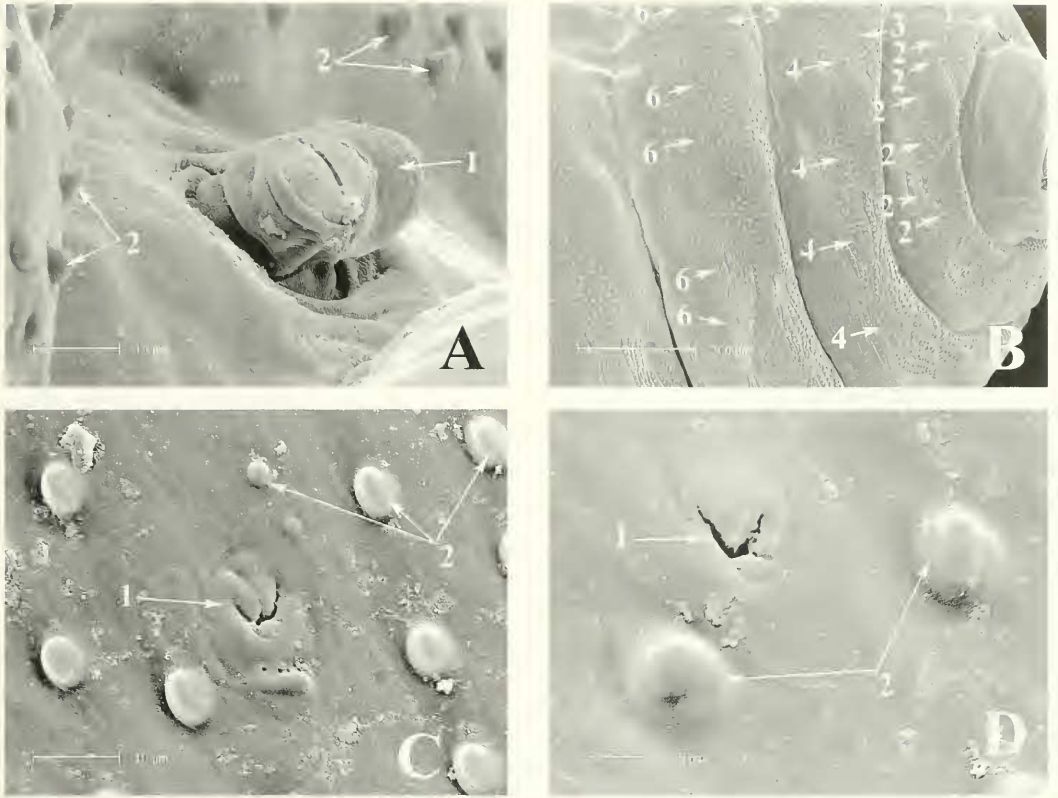


Fig. 2. Third instar of *Goedenia stenoparia*, continued: (A) 1—anterior spiracle, 2—minute acanthae; (B) lateral spiracular complexes, anterior to right, 1—anterior spiracle, 2—verruciform sensilla on mesothorax, 3—lateral spiracle on metathorax, 4—verruciform sensilla on metathorax, 5—lateral spiracle on first abdominal segment, 6—verruciform sensilla on first abdominal segment; (C) close-up of lateral spiracle on metathorax, 1—spiracle, 2—minute acanthae; (D) close-up of lateral spiracle on first abdominal segment, 1—spiracle, 2—minute acanthae.

2002b) and *G. stenoparia* anteriorly bear a few minute acanthae (Figs. 1D-1). Two medial and four lateral integumental petals are present in *G. stenoparia* (Figs. 1E-7, 8, F-1), as in *G. rufipes* (Goeden 2002a); whereas, *G. timberlakei* has six lateral integumental petals (Goeden et al. 1995, unpublished data) and *G. setosa* has five (Goeden 2002b). The lateral-most integumental petal is separated from the stomal sense organ in all four species (Fig. 1F-3; Goeden et al. 1995; Goeden 2002a, b).

The third instars of all four species of *Goedenia* studied to date lack oral ridges on either side of the mouth opening, and ventral or ventrolateral to the stomal sense

organ (Figs. 1D, E, F; Goeden et al. 1995; Goeden 2002a, b, and unpublished data).

The mouthhooks of the third instars of *G. stenoparia* (Figs. 1D-7, F-2), like those of *G. timberlakei* (Goeden et al. 1995), *G. rufipes* (Goeden 2002a) and *G. setosa* (Goeden 2002b), are bidentate. Moreover, a ventral view of the oral cavity (Fig. 1F), like that figured and described for *G. rufipes* (Goeden 2002a), but not obtained for either *G. timberlakei* (Goeden et al. 1995, unpublished data) nor *G. setosa* (Goeden 2002b), showed the concavely scalloped, posterior surface of the anterior tooth (Fig. 1F-4).

The anterior spiracle of all four *Goedenia*

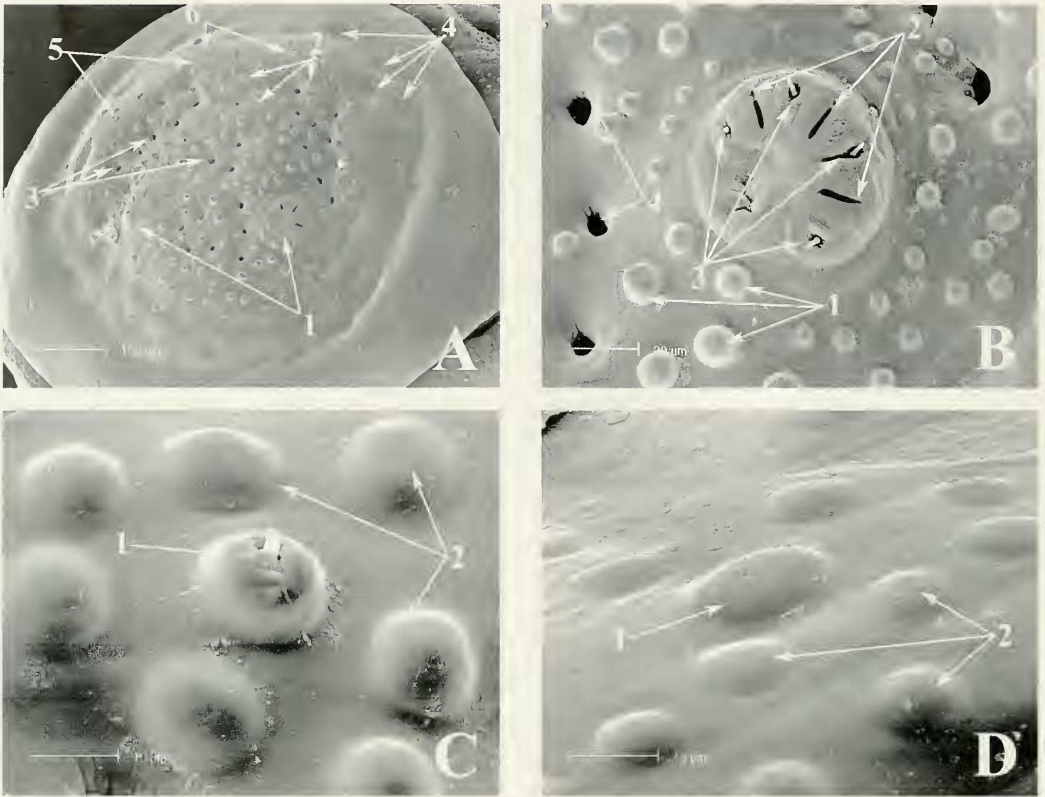


Fig. 3. Third instar of *Goedenia stenoparia*, continued: (A) caudal segment, 1—posterior spiracular plates, 2—minute acanthae, 3—pores, 4—shallow, elliptical depressions, 5—stelex sensilla, 6—verruciform sensillum; (B) posterior spiracular plate, 1—minute acanthae, 2—rimae, 3—interspiracular processes, 4—pores; (C) 1—stelex sensillum, 2—minute acanthae; (D) 1—verruciform sensillum, 2—minute acanthae.

species bears only two papillae (Figs. 1C-4, 2A-1; Goeden et al. 1995, Goeden 2002a, b).

The lateral spiracular complex of the mesothorax of *G. stenoparia* includes six verruciform sensilla in a vertical series (Fig. 2B-2) like that of *G. rufipes* (Goeden 2002a); whereas, in *G. timberlakei*, this same complex includes only two verruciform sensilla (Goeden et al. 1995). Likewise, the metathoracic lateral spiracular complex of *G. stenoparia rufipes* includes four verruciform sensilla (Fig. 2B-4), again like *G. rufipes* (Goeden 2002a); whereas, only two such sensilla occur in *G. timberlakei* (Goeden et al. 1995). Finally, five verruciform sensilla in a vertical series comprise the lateral spiracular complex of the first abdominal segment of *G. stenoparia*

(Fig. 2B-6), three such sensilla occur in *G. rufipes* (Goeden 2002a), but only one verruciform sensillum is found on this segment in *G. timberlakei* (Goeden et al. 1995).

*Puparium*: Light to dark, reddish brown with dark brown to black, anterior stripe or series of spots on venters of meso- and metathorax and abdominal segments A-1 to A-4 (Fig. 5E), and similarly dark, caudal segment, elongate-ellipsoidal, with smoothly rounded anterior end, and truncated posterior end (Fig. 4A). Anterior end bears invagination scar (Fig. 4B-1) and raised, bilobed, anterior thoracic spiracles (Fig. 4B-2). Flattened posterior end of caudal segment studded with smoothly rounded, hemispherical, minute acanthae (Figs. 4C-1, D-1) interspersed with open pores (Figs. 4C-2, D-2). A pair of raised, hemispher-

idal, posterior spiracular plates (Fig. 4C-3) each bear three elliptical rimae interspersed with four peg-like, interspiracular processes. These structures are ringed by shallow, elliptical depressions (Fig. 4C-4). Twenty-three puparia dissected from flower heads of *Gutierrezia californica* and *Solidago californica* averaged  $2.66 \pm 0.07$  (range, 1.92–3.27) mm in length;  $1.16 \pm 0.02$  (range, 0.99–1.42) mm in width.

#### DISTRIBUTION AND HOSTS

Foote et al. (1993) mapped the distribution of *Goedenia stenoparia* as southwestern California along with one location in southwestern Utah, which suggests a widespread distribution for this tephritid in western North America north of Mexico. The collective distributions of the host plants listed below also would indicate such a wide distribution for *G. stenoparia*, which probably also encompasses northern Mexico (Hickman 1993).

*Goedenia stenoparia* was reported as reared from *G. microcephala*, *Gutierrezia sarothrae* and *Ericameria cuneata* (as *Haplopappus cuneatus*) (A. Gray) McClatchie by Goeden (1987). Foote et al. (1993) reported these rearing records along with a sweep record from *Hymenoclea salsola* Torrey and Gray, a non-host (Goeden and Ricker 1986), which Goeden (1987) used to illustrate the often misleading or useless nature of sweep records—no matter how accurately the plant and tephritid are identified! *Gutierrezia californica* and *Solidago californica* were newly reported in this paper as hosts, as are *E. parishii* (E. Greene) H. M. Hall, *Hazardia squarrosa*, and *Lesingia glandulifera* A. Gray. All of these new host records for *Goedenia stenoparia* are from southern California. All of the aforementioned hosts belong to the family Asteraceae, tribe Astereae, subtribe Solidagininae (Bremer 1994), as do all other reported and confirmed hosts of *Goedenia* spp. (Goeden 1987, Freidberg and Norrbom 1999). Accordingly, *G. stenoparia* is classed as narrowly oligophagous (on eight

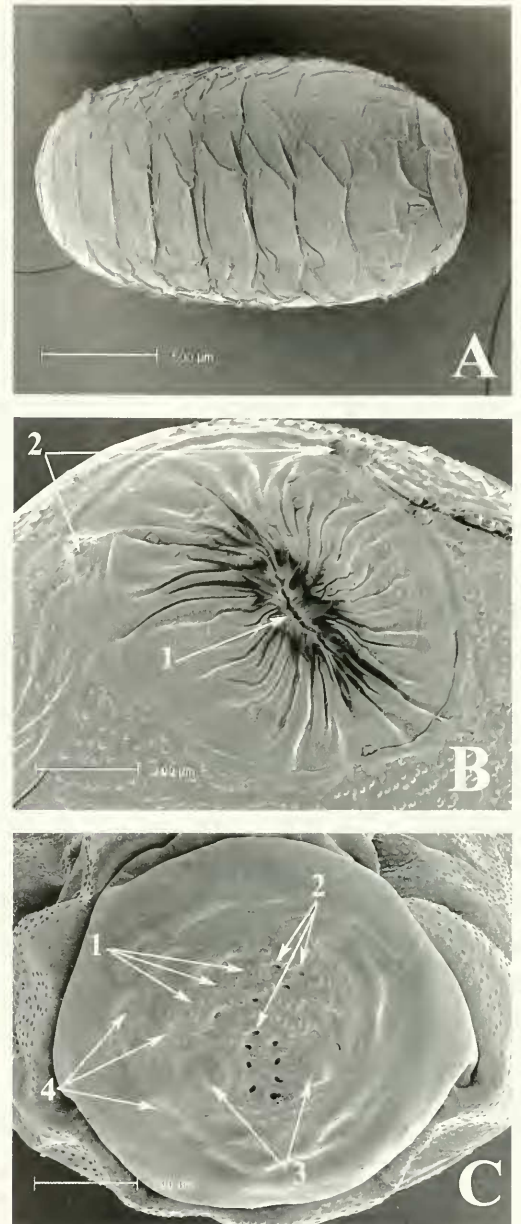


Fig. 4. Puparium of *Goedenia stenoparia*: (A) habitus, anterior to right, (B) anterior end, 1—invagination scar, 2—anterior spiracles; (C) caudal segment, 1—minute acanthae, 2—pores, 3—posterior spiracular plates, 4—shallow, elliptical depressions.

species of one host subtribe in the Asteraceae) (Goeden 1987, Headrick and Goeden 1998).

As noted above, their host plants also





serve to distinguish *Goedenia formosa* and *G. caurina* from *G. stenoparia*, at least in southern California. My current opinion is that *G. formosa* is now known only from *Isocoma menziesii* (Hooker and Arnott) G. Nesom, formerly treated by Munz (1974) as two varieties of *Haplopappus venetus* (von Humboldt) Blake, and reported as such as hosts by Goeden (1987). Additional hosts for *G. formosa* reported by Wasbauer (1972) and Goeden (1987) should refer to either *G. stenoparia*, as noted above, to *G. caurina*, or to an undescribed *Goedenia* from *Grindelia* spp. (my unpublished data). Consequently, *G. caurina* currently is recognized by me as reared from *Chrysothamnus parryi* (A. Gray) E. Greene, *C. viscidiflorus* (Hooker) Nuttall, *Ericameria ericoides* (Lessing) Jepson, and *E. palmeri* (A. Gray) H. M. Hall (Goeden 1987, unpublished data). Unfortunately, my coworkers and I did not study *G. caurina* or *G. formosa* in the aforementioned hosts, as their taxonomic distinction from *G. stenoparia* was only recently better clarified, as reported above.

#### BIOLOGY

**Egg.**—No flower head of *Gutierrezia californica* containing an egg of *Goedenia stenoparia* was sampled; however, it is assumed that a single egg is inserted into each young preblossom flower head based upon dissections of flower heads each containing a single larva as reported below. The few, solitary eggs observed in very young, closed preblossom heads of *Solidago californica* supported this assumption (Fig. 5A); however, a cluster of three eggs found within the apical leaves covering a young, compound, terminal inflorescence of *S. cal-*

*ifornica*, also containing very small, preblossom flower heads (buds) (Fig. 5B) indicated an alternative mode of oviposition for this tephritid. None of these eggs were inserted within plant tissues, observations supported by empty chorions found adjacent to newly eclosed first instars observed within a few other stem terminals.

**Larva.**—Upon eclosion from the egg, each first instar commenced to feed separately within a fast-developing, preblossom flower head on the florets therein. The receptacle was neither abraded or pitted by such feeding.

Single second instars were found feeding on ovules in eight, separate, closed, preblossom flower heads of *Gutierrezia californica* (Fig. 5C). They usually fed within an ovule with their bodies perpendicular to, but always above, the receptacles (Fig. 4A). Receptacles of the eight flower heads containing second instars averaged  $0.62 \pm 0.03$  (range, 0.57–0.71) mm in diameter. These larvae had damaged an average of  $3.0 \pm 0.7$  (range, 2–4) ovules, or about 46% of the average total of  $6.5 \pm 0.4$  (range, 5–8) ovules counted within each of the eight flower heads. However, 516 flower heads were individually dissected in order to locate these eight flower heads infested with second instars (Fig. 5C).

Likewise, single second instars were found feeding on ovules in 11 separate, closed, preblossom flower heads of *S. californica* (Fig. 5C). All were found within adjacent flower heads on several compound inflorescences, again indicative of oviposition of eggs in clusters. They, too, usually fed on ovules with their bodies perpendicular to, but always above, the receptacles (Fig. 5C). Receptacles of the 11 flower

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Fig. 5. Life stages of *Goedenia stenoparia* in flower heads of *Gutierrezia californica* and *Solidago californica*: (A) single egg (arrow) in *S. californica*; (B) three eggs (arrows) in *S. californica*; (C) second instar (arrow) in *S. californica*; (D) third instar feeding in receptacle having consumed other contents of flower head of *G. californica* (note dark infuscation on venter); (E) third instar in *S. californica*; (F) puparium in flower head of *G. californica*; (G) mating pair, dorsal view; (H) mating pair, lateral view; (I) unreceptive female depressing oviscape to avoid coitus. Lines = 1 mm.

heads containing second instars averaged  $1.00 \pm 0.04$  (range, 0.85–1.14) mm in diameter. These larvae had damaged an average of  $2.1 \pm 0.3$  (range, 1–4) ovules, or about 46% of the average total of  $10.6 \pm 1.3$  (range, 8–15) ovules counted within each of the 11 flower heads.

Third instars fed with their long axes oriented perpendicular to the receptacles, and with their mouthparts directed towards the receptacles, which they scored or pitted, lightly when young to deeply when fully grown, in all of 38 infested flower heads examined of *G. californica* (Fig. 5D). The 38 flower heads (10 closed preblossom; 28 dead, overwintered) each contained a single third instar (Fig. 5D). These 38 flower heads averaged  $0.75 \pm 0.03$  (range, 0.85–1.42) mm in diameter and contained an average of  $8.9 \pm 0.2$  (range, 4–11) ovules/achenes, all of which were damaged or completely destroyed by the time of prepupariation (Fig. 5D).

Similarly, third instars fed as above in all of 50 infested flower heads examined of *S. californica* (Fig. 5E). The 50 flower heads (7 closed preblossom or 43 at least partly open, postblossom and senescent or dead and overwintered) each contained a single third instar. These 50 flower heads averaged  $1.14 \pm 0.02$  (range, 0.42–0.85) mm in diameter and contained an average of  $17.2 \pm 0.5$  (range, 12–22) ovules/achenes, all of which were damaged or completely destroyed by the time of prepupariation (Fig. 5E).

Pitted receptacles in both of the above host species (Figs. 5D, E) suggest that sap constitutes at least part of the diet of third instars of *G. stenoparia*, as reported also for *G. timberlakei* (Goeden et al. 1995), *G. rufipes* (Goeden 2002a), and *G. setosa* (Goeden 2002b). Goeden (1988), Headrick and Goeden (1990), Goeden and Headrick (1992), Goeden et al. (1995), Headrick et al. (1996), and Goeden and Teerink (1997) also first noted, described, and discussed sap feeding by florivorous species of Tephritidae in the genera *Trupanea*, *Paracan-*

*tha*, *Neaspilota*, *Tephritis*, *Dioxyina*, and *Xenochaeta*, respectively. Upon completing feeding in flower heads of *Gutierrezia californica*, the larva constructed a vasiform cell consisting of ovule/achene/floret fragments impregnated with and hardened by dried, liquid feces and sap. The wall of these cells in *S. californica* was noticeably thinner than in *G. californica*. The flattened, sclerotized caudal segment of the third instar nicely serves as a plug that tightly closes the mouth of the cell, yet allows respiration, and thus apparently also may serve to shield the larva from arthropod predators (but certainly not parasitoids, see below) during overwintering (Goeden 2002b). Prior to pupariation the prepupa turns 180° and orients with its anterior end away from the receptacle, retracts its mouthparts, and forms a puparium (Figs. 5F).

Pupa.—Infested, overwintered flower heads each contained a single puparium (Figs. 5F). The posterior of the puparium faced the receptacle, rested in the cuplike base of the cell, and all but the anterior part of the puparium tightly adhered to the inner wall of the cell in *G. californica* (Fig. 5F). However, puparia in *S. californica* flower heads were only loosely confined.

Adult.—Under insectary conditions, 45 males of *G. stenoparia* lived an average of  $28 \pm 2.5$  (range, 7–77) days, and 31 females lived an average of  $25 \pm 2.6$  (range, 6–53). These longevities were less than the mean longevities reported for *G. timberlakei* (Goeden et al. 1995) and *G. setosa* (Goeden 2002b), but still are commensurate with the aggregative type of life histories possessed by all three of these tephritids (Headrick and Goeden 1994, 1998; Goeden et al. 1995).

The pre mating and mating behaviors of *G. stenoparia* were not studied in the field, but were observed for five pairs (one male and one female each) reared from *Gutierrezia californica* and 10 pairs from *S. californica* in separate petri dish arenas. These arenas were of the type found to be useful in studying mating behaviors of many other

nonfrugivorous, tephritid species (Headrick and Goeden 1994). Both sexes exhibited wing hamation (Headrick and Goeden 1994) throughout the day concurrent with other behaviors, i.e., grooming, resting, and feeding; this also was the most common wing movement reported for *G. timberlakei* (Goeden et al. 1995), *G. rufipes* (Goeden 2002a), and *G. setosa* (Goeden 2002b). Premating behaviors observed with *G. stenoparia* included males and females tracking individuals of the opposite sex, during which males sometimes swayed and usually exhibited abdominal pleural distension. During mating, the wings of the male were overlapped (Fig. 5G) or parted at 10–60°, the wings of the female were parted at 60–90° (Fig. 5G), with both pairs of parted wings centered over the midline of each fly (Figs. 5G). The foretarsi of the male grasped the dorsum of the abdomen of the female laterally at the thoracic juncture, the midtarsi grasped the abdomen laterally or the oviscapae at its base, and the hindtarsi crossed under the oviscapae (Fig. 5H). The bodies of both flies paralleled the substrate with the oviscapae elevated about 45° (Fig. 5H). In arenas, the flies mated at least once on successive days at different times during daylight; six pairs were observed to mate twice in one day. Another especially active pair was observed mating 28 times on 21 consecutive days, after which, the female died. A total of nine matings were observed that lasted an average of 128 (range, 38–312) min. Mating females were observed to walk about the arenas, to groom, drink, and form droplets (Headrick and Goeden 1994, 1998). Females became restless before termination of mating and pushed against the males with their hind tarsi, they also lofted their wings so as to push against the males and fully extended their aculei. The male in turn countered this agonistic behavior with copulatory induction behavior (CIB), i.e., rubbed his hind tarsi along the oviscapae, grasped the female tightly, rocked from side to side to regain purchase or to avoid the female's pummeling, and sometimes rapid-

ly vibrated his wings, all of which appeared to calm the female and allow coitus to continue. During postcoital separation, the male turned and rapidly walked off and away from the female while pulling his genitalia free, a process lasting just 5 and 8 s in two cases. Nonreceptive females avoided matings by decamping, by deflexing their oviscapae to the substrate (Fig. 5I) or otherwise by physically preventing males from gaining purchase by means of agonistic behaviors described above.

Seasonal history.—The life cycle of *Goedenia stenoparia* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the prepuparia, puparia, and a few adults variously are the overwintering stages. Some adults emerged from a few puparia formed in late-fall (October–November) and these unmated, sexually immature adults overwinter. The remaining prepuparia and puparia overwinter in cells in dead flower heads that remain attached to dead inflorescences of *Gutierrezia californica*, *S. californica*, and presumably the other hosts of *Goedenia stenoparia*. These overwintered individuals emerge as adults in spring (April–May) and pass the following summer (June–September), probably as non-reproductive individuals in riparian habitats. They eventually aggregate on preblossom, fall-blooming, host plants, to mate, and subsequently to oviposit in or alongside of the small, newly-formed, closed, preblossom flower heads.

Natural enemies.—Overwintered puparia of *G. stenoparia* were parasitized by chalcidoid Hymenoptera in the genera *Eurytoma* (Eurytomidae), *Pteromalus* (Pteromalidae), and *Torymus* (Torymidae) as probable primary, solitary, larval-pupal endoparasitoids.

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